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Modelling a forest lepidopteran: phenological plasticity determines voltinism which influences population dynamics

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Abstract

Mnesampela privata is an Australian geometrid moth that is considered to have resource-driven outbreaks. An autumnal oviposition/larval development cycle is considered the "norm" in this species, but spring/summer activity has also been observed. This apparent plasticity of phenology and probable concomitant changes in voltinism have not been considered as possible causes of moth outbreaks. We developed GumMoth, a retrospective phenological model for M. privata that uses temperature to predict development times of immatures. Photoperiod determines whether individuals undergo direct development or pupal diapause. We used known catch dates of moths (in the same moth-active season or 365-day period) to simulate population phenologies on the Australian mainland (27°28'S to 38°14'S) and in Tasmania (40°54'S to 42°57S). GumMoth successfully simulated phenological patterns that accorded with published records and demonstrated for the first time that multivoltinism is possible in M. privata. In seven paired simulations using dates for first and last moth catches, the earliest moth activity resulted in the pupae of four out of 11 generations undergoing diapause, whereas the latest moth activity resulted in pupae of five out of eight generations undergoing diapause (diapause individuals emerged the following moth-active season). Almost two-thirds of offspring of spring/summer active moths reached adulthood within that same moth-active season (i.e. no delay in development), whereas those of autumn active moths always reached adulthood the following moth-active season (i.e. development was delayed). Records from foresters and in the scientific literature confirmed that the more common autumn phenology is supplemented by spring/summer activity in many localities. At half of these localities, populations that required insecticide control or caused substantial defoliation also developed. Because plantation eucalypts are suitable M. privata hosts for only four to five tree-growth seasons after planting, local moth populations must increase quickly if an outbreak is to occur. We suggest that large populations are more likely when plantations

are colonised in the first moth-active season after planting and population growth commences in the spring/summer of each year. Foresters can use catch dates and regional weather data in GumMoth to estimate the numbers and phenology of generations of M. privata. This information can be used to assess risk posed by regional populations and thereby adjust future surveillance intensity.

Keywords: DYMEX; Eucalyptus; Mnesampela privata; Seasonal phenology; Metapopulations; Insect management

1. Introduction

Bluegums (i.e. Eucalyptus globulus globulus and E. nitens) are grown, in Tasmania, southern Victoria, southern South Australia and south-west Western Australia, predominantly for woodchips. Currently, bluegum plantations cover 311,000 ha and are being established at the rate of 116,000 ha annually (National Forest Inventory, 2002). A variety of insect pests are of concern to foresters in different regions, however, the larvae of the autumn gum moth (Mnesampela privata (Guenée)) are considered among the most important insect defoliators of plantation bluegums across almost all the regions where commercial operations are conducted (with the possible exception of south-west Western Australia). The primary reason for their concern is that populations of M. privata can outbreak and cause whole-tree defoliation of entire plantations (Lukacs, 1999; Steinbauer et al., 2001). Spatial and temporal variation in the incidence of M. privata contributes further to foresters' concern as it hinders the formulation of surveillance schedules that can be applied with confidence across all forestry districts and states where plantation eucalypts are grown.

Mnesampela privata is called the autumn gum moth because significant damage to leaves generally becomes apparent during autumn (e.g. Roberts and Sawtell, 1981; McFarland, 1988; Neumann, 1993; Abbott, 1993; Farrow et al., 1994). Adults emerging in autumn commence oviposition almost immediately and their larvae develop through autumn into winter, before entering the soil to become diapausing pupae. Pupae have a hormonally induced diapause that may be supplemented by temperature-induced aestivation (either prior to adult differentiation or as unpigmented pharate adults or both) (Lukacs, 1999). Many pupae aestivate over the summer months and eclose in autumn starting the next generation. However, earlier adult emergence is also possible, i.e. adults emerge soon after diapause finishes without entering a period of pupal aestivation. It is the interplay between diapause,

aestivation and the environment that enables M. privata to exhibit a variable phenology across regions in any one year (Lukacs, 1999).

Outbreaks of M. privata are not known to occur in native forests (Steinbauer et al., 2001). In plantations, however, M. privata displays population dynamics that have many of the traits of the sustained gradient (i.e. resource-driven) outbreaks of other insect species (Berryman, 1987). That is, an abundance of bluegums, later combined with repeated oviposition on hosts already supporting conspecifics, generates large localised (i.e. confined by the area of the plantation) populations (Steinbauer et al., 2001). If plantations of bluegums were always suitable for oviposition and larval development then outbreaks of M. privata would be inevitable at some time during their growth. Fortunately for foresters, eucalypts are heterophyllous and most of the leaves in the canopies of both E. g. globulus and E. nitens phase change to adult foliage some three to four years after the seedlings are planted (Jordan et al., 1999). Females prefer not to lay eggs on adult foliage, possibly because the toughness of these leaves reduces the performance of neonates (Steinbauer, 2002).

Mnesampela privata has usually been described as univoltine (Lukacs, 1999), although as mentioned above, there have also been reports of spring/summer activity, indicating that the univoltine phenology may not be the only possible pattern of activity (Froggatt, 1923; Elliott and Bashford, 1978; McFarland, 1988; Farrow, 1996). For the most part, however, spring/summer activity appears to have gone unnoticed or been considered of no ecological or commercial significance. This situation is changing as more foresters notice that populations of larvae reach numbers requiring insecticide control sooner than expected, i.e. because activity began in spring/summer and went unnoticed by them. Given such instances, we think it necessary to reconsider the significance of spring/summer activity in M. privata. The intentions of this paper were to (1) develop a phenological model for M. privata using data from Lukacs (1999) to simulate phenology and population development, as a function of

temperature and photoperiod; (2) document the incidence of spring/summer activity and; (3) consider the possible role of phenological plasticity on voltinism and population dynamics.

2. Materials and methods

2.1. MODELLING PHENOLOGY AND VOLTINISM

The model

We used DYMEX™ to create GumMoth, a model to simulate the numbers of generations of M. privata and their phenology in different regions of Australia. DYMEX is a modelling package that supports the rapid development of mechanistic or process-based cohort models (Maywald et al., in press). While it is possible to develop detailed process-based population dynamics models using DYMEX (Kriticos et al., 2003; Yonow et al., 2004), it is also possible to use the package to build and run simple development rate models, largely ignoring population demography (e.g., Farr, 2002).

In DYMEX, life cycles consist of one or more life stages that contain cohorts of individuals (Fig. 1). Cohorts are created in each time-step (in this case each day) in which one or more individuals progress to a new life stage. Cohort attributes such as chronological age and physiological development of cohorts are tracked by DYMEX along with any user-defined attributes (e.g. accumulation of diapause-inducing conditions).

Egg and larval developmental rates were estimated from original data in Lukacs (1999). Lukacs' data was derived from observations of the development of individuals from recently laid eggs through to pupation at constant temperatures. These individuals were the offspring of a female moth from near Surrey Hills in northwest Tasmania (see Results for location details). Lukacs (1999) compared developmental rates of this female's offspring with those of a female from Cobram in northern Victoria (35°55'S 145°44'E, 110 m a.s.l) and found minimal differences between the two. Egg and larval developmental rates obtained by

Schumacher (1997) using insects collected from Canberra were comparable with those in Lukacs (1999). Note, ZL also found no significant differences in the developmental rates of eggs of 14 families of *M. privata* from Tasmania when reared at four constant temperatures in the range between 10-25°C (unpubl. data).

Lukacs (1999) did not include developmental rates for individuals exposed to supra-optimal temperatures, however, of 120 eggs kept at 30°C none eclosed even though some initial embryonic development occurred (ZL, pers. obs). In GumMoth, developmental rates for eggs and larvae at temperatures above those employed by Lukacs (1999) were reduced linearly from the assumed optimal development temperature of 24°C to zero at 30°C. The analytical method involved calculating for each temperature, the duration in the stage, or combination of stages, and the developmental rate per day (inverse of the duration in a stage). A linear regression model was fitted to the developmental rate as a function of temperature for each of the defined life stages. The developmental base temperature (x-intercept, referred to hereafter as T_o) was calculated using the regression equation. The daily developmental heat summation for each individual was then calculated by multiplying the duration in a stage by the constant temperature less the base temperature. The mean and standard deviation of the required developmental heat summation was then calculated for each life cycle stage. The heat sum transfer limits were estimated by taking the mean and subtracting twice the standard deviation (2*SD) to estimate the lower limit and adding 2*SD for the upper limit. A linear-above-threshold transfer function was used to describe the daily proportion of the remaining individuals in a cohort that would transfer to the next stage. This function used a threshold of the lower heat sum limit and a slope equivalent to the inverse of 4*SD (upper – lower heat sum limits); commencing stage transfer at the lower heat sum threshold, and completing it at the upper heat sum threshold. The resulting pattern of transfer is a right-skewed bell-curve

that accords with observations by Lukacs (1999). Developmental rates for non-diapausing pupae were taken directly from Lukacs (1999).

Table 1 summarises the developmental data used to build GumMoth. In GumMoth we assume that pupal diapause is initiated sometime during the first to fourth larval instar if a user-definable minimum number of days (default 7) are spent at photoperiods < 12 hrs (between the autumn and spring equinoxes). Consequently, all first to fourth instar larvae that develop after late March and before mid September will, according to our model, undergo diapause, while those first to fourth instar larvae that develop after mid September but before late March will undergo continuous development. The larval instar and critical photoperiod that trigger the onset of diapause are based on experience rearing this insect gained by ZL (see next).

The duration of pupal diapause in M. privata decreases linearly from the autumn equinox to at least mid-November (Lukacs, 1999). The duration of diapause is negatively correlated with the length of time that immature larvae (i.e., first to fourth instar) are exposed to short days (< 12 hrs photoperiod; Fig. 2). This has the effect of narrowing the time period over which diapause pupae become adults. Lukacs' diapause duration model is based on the number of days since the autumn equinox and predicts the total length of time taken for diapause and adult differentiation (291d – 0.6223*[days from autumn equinox]). In GumMoth, Lukacs' phenological model was transformed into a process-based function of the total number of short days (< 12 hrs photoperiod) experienced by first to fourth instar larvae:

$$D_d = 256 - 2.3D_s \qquad \text{Equation 1}$$

where D_d is the diapause duration, and D_s is the number of short days (< 12 hrs photoperiod) that immature larvae experience.

Equation 1 was derived from Lukacs' regression equation (given above) by firstly subtracting the period of adult differentiation from the intercept. This was necessary because

GumMoth distinguishes between diapause and adult differentiation. The intercept is the maximum number of days of diapause that is experienced by an individual that has experienced the minimum number of short days necessary to trigger diapause development when a larva. We assume that exposure of larvae to seven short photoperiod days will trigger diapause. Model simulations show that the maximum cohort duration for first to fourth instar larvae (approximately 62d) occurs for larvae that emerge in mid-June (southern hemisphere). Assuming that the photoperiod counter is restricted to this set of instars, the range of token sampling is seven to 62d. The pupae from this winter cohort underwent a diapause of approximately 115d (Lukacs, 1999). The slope was therefore calculated as (115-256)/(62-7).

Shortly after the autumn equinox, $\underline{D_S}$ is limited by the number of days since the equinox. As temperatures decrease, larval duration increases, and the maximum duration is reached when the whole larval duration is spent at daylengths <12 hrs, so that $\underline{D_s}$ becomes the length of time spent as a larva. The larval duration peaks for larvae that hatch around the winter solstice and according to the model, the diapause duration starts to increase again for larvae that hatch after this time. In post diapause pupae, an aestivation is initiated (i.e. physiological development is temporarily suspended) if temperatures rise above 19°C (Lukacs, 1999).

A circadian temperature model is used to drive all temperature-related functions in GumMoth. In this case the circadian module fits a composite sine and exponential function to the daily minimum and maximum temperature data in order to estimate temperatures for each hour. GumMoth totals the development heat sum for each of these segments, providing a suitable translation between the constant temperature development rate observations and the variable temperature environment being simulated. We obtained weather data to use in the model from the Silo Data drill website (see http://www.nrm.qld.gov.au/silo/datadrill/datadrill_frameset.html). These data are spatially

(and occasionally temporally) interpolated and do not exactly equate with temperatures that might be recorded in a Stevenson screen for a particular locality.

Based on light trap catches and field observations by Lukacs (1999) and Steinbauer (2003), we assume that the 'moth-active season' typically extends from November to May. Consequently, where moth-active season is used in the text we are referring to these months. A pair of simulations is shown in Fig. 3 to illustrate the graphical output from GumMoth.

Model predictions based on first and last catches within a moth-active season

We made seven paired sets of GumMoth simulations for populations of M. privata using known dates for the first and last catches of adults caught during a single moth-active season. These two dates were used as starting dates for each pair of simulations. The purpose of these paired simulations was to examine resultant population phenologies for offspring, the only difference being the onset of their development. We assumed that for each catch date a single female was present nearby and laid 100 eggs. We then modelled population development and phenology for 365d after that date. Female moths are assumed to have a total fecundity of 300 eggs (see Steinbauer et al., 2001; not all laid on one occasion). For clarity in assessing phenological patterns, fecundity was set to 1 egg per adult moth, and cohorts were terminated when they had less than $1/300^{th}$ of an individual remaining. This had the effect of ensuring that the population remained stable from year to year, while still reproducing appropriate phenological variation.

2.2. DOCUMENTING AND MAPPING SPRING/SUMMER ACTIVITY

Experienced foresters were asked about locations where spring/summer (Australian spring = September to November and summer = December to February) activity had been observed (N.B. autumn = March to May and winter = June to August). Additional records of

spring/summer activity from the scientific literature were also collated. Whenever possible, details concerning latitude and longitude, elevation above sea level (a.s.l.) and years in which spring/summer activity had been observed were recorded. When latitude and longitude details for locations were not known, we used the next closest grid reference available from the Master Names File (MNF) of Australian localities (originally compiled by the Australian Surveying & Land Information Group). If elevations for locations were not known we made the best estimate possible by examination of 1:100,000 topographical maps.

3. Results

3.1. MODELLING PHENOLOGY AND VOLTINISM

GumMoth predicts adult activity in the same calendar months as given by Lukacs (1999) and Steinbauer (2003). However, the model also predicted some adult activity in July and August onwards as well as in October (Table 2). These are months in which sampling for M. privata by Lukacs (1999) and Steinbauer (2003) was not conducted and as a consequence it is not possible to validate activity in these months. However, moths have been caught in August (see Stoney Rise in Table 2) so it is possible that very small numbers of moths may be around at almost all times of the year. The authors (unpubl. data) have certainly noted that larvae maybe collected at anytime of year, although they are generally uncommon in late winter and early spring.

The model simulates multivoltinism in M. privata. Of the seven paired simulations in Table 2, four (1a, 3a, 4a and 7a) reveal that M. privata will achieve more generations within a 365-day period if population development commences early in the moth-active season. Using the first catch dates (which includes five dates in spring and two dates in summer), we found that only four out of 11 generations (in seven simulations) would undergo pupal diapause (Table 2). This contrasts with five out of eight generations (in seven simulations) when the

last catch date was used (which includes two dates in summer, three dates in autumn and two dates in winter). Notice that the incidence of diapause for simulations grouped according to season ranged between 29% (two out of seven generations), 50% (three out of six generations), 100% (three out of three generations) and 33% (one out of three generations) for spring, summer, autumn and winter, respectively (Table 2).

In two of the locations in Tasmania, M. privata may have required > 365d to reach adulthood (Table 2). Such predictions suggest that adult activity would be shifted by a month or two into the next moth-active season under the temperatures that occurred at those locations and during those years. Given the many interactions that could influence any particular individual during its lifetime we do not think readers should attempt to consider the possible phenological implications for such shifts in adult activity (hence our use of a 365-day period throughout most of this work).

It is important to remember that moths have been caught at times other than the first and last catch dates presented in Table 2. Consequently, within the same moth-active season, late instar larvae destined to undergo direct development (i.e. non-diapause) must overlap with early instar larvae destined to diapause. While it is possible in GumMoth to initialise simulations with more than one cohort, for clarity, only single oviposition scenarios have been presented.

3.2. DOCUMENTING AND MAPPING SPRING/SUMMER ACTIVITY

Instances of spring/summer activity have been recorded from 18 disparate locations within the region of endemism of M. privata (Fig. 4), although spring/summer activity appears absent (or has not been recorded) in south-west Western Australia. The locations in Table 3 exhibit a range of elevations from just above sea-level to above 600 m. Spring/summer flights of moths occur at sea-level in many parts of Tasmania as is demonstrated by the presence of third and

fourth instar larvae at Stanley (less than 10 m a.s.l) in mid February (MJS and Fredrik Östrand, 2003, pers. obs). These reports indicate that spring/summer activity is not exclusive to high altitude locations, i.e. places above 500 m (as suggested by Lukacs, 1999). Spring/summer activity does not appear to necessarily occur each year at any given locality where it was previously recorded (Table 3). For example, spring/summer activity was not observed at Wallaroo Road during 2002/03 (MJS, pers. obs.).

Of the 18 locations where spring/summer activity has occurred, three have experienced serious outbreaks and six have had sufficiently large populations of larvae to warrant insecticide control (Table 3). Censuses of populations of moths and larvae at the other locations were not provided and as a consequence it is not possible to comment upon their size or impact.

4. Discussion

GumMoth produced simulations of phenology that match closely the recorded phenology of M. privata even though the larval instar and critical photoperiods that induce diapause have yet to be determined through experimentation. At present, GumMoth assumes that if a cohort of first to fourth instar larvae experiences seven short photoperiod (< 12 hrs) days, diapause development will occur following pupation. These criteria were based on observations of the development of 1211 pupae, 480 of which successfully eclosed, that were collected from the wild at various times of year during the 1995 to 1997 moth-active seasons as late fifth instar larvae by ZL. It was repeatedly observed that if larvae were collected before mid-March, pupal development would be completed after just 2-3 months. In contrast, if larvae were collected at an apparently critical period around mid-March, pupal development would take 8-10 months, i.e. the seasonal maxima. Larvae collected after this time required 4-5 months of pupal development (see Fig. 2; phenomenon of declining diapause duration

considered by Danks, 1994). Given that the autumnal equinox occurs on the 20th or 21st of March in the southern hemisphere, we assumed that the length of the photoperiod experienced by these larvae prior to their collection determined the "switching time" (sensu Taylor, 1986) between direct or diapause development. The importance of photoperiod as a token stimulus for diapause induction in insects has been well documented (Beck, 1968; Denlinger, 1985). Because these observations suggested that the stimulus for diapause initiation occurred before the fifth instar and GumMoth only compartmentalises larval development into either first to fourth or fifth to pre-pupal cohorts (Fig. 1), we were required to adopt the criteria specified above. Earlier preliminary experimental studies indeed suggest that the larval stadia that maybe sensitive to photoperiods < 12 hrs are the first and second larval instars (Rapley, 1998). At this stage we have no cause to suspect that density dependent diapause may occur in M. privata (e.g. Geri and Goussard, 1989)

Confidence in a process-based cohort model is gained primarily from running it for a variety of scenarios and comparing the output with observed phenomena from circumstances that are judged to adequately correspond to the model scenario (e.g. Table 2). Another technique is to undertake model sensitivity analyses. Sensitivity analyses involve gauging the effect of altering the value of a model parameter on a state variable(s). The greater the change in the value of the selected state variable for a given proportional change in the value of a parameter, the greater the sensitivity of that parameter. Sensitivity analyses indicate the effect of inaccurately estimating a parameter, and therefore provide an understanding of how important it is to have reliable and precise estimates for each parameter. It is more important to have reliable estimates for the more sensitive parameters than it is for relatively insensitive parameters. A critical component of a sensitivity analysis is the selection of state variables that adequately characterise those aspects of the model that are of interest. GumMoth is a phenological model, so we chose the length of time (days) from the date of the first observed

egg batch until the first adult emergence (A) as the dependent state variable. We altered the value of parameters by ± 5% in order to gauge the effect of a 10% change in the parameter values. While it is generally not a good idea to choose a single state variable as a general indicator of model behaviour (Miller, 1974), the chosen state variable integrates the behaviour of the rest of the model and is pertinent to the insect's phenology which is of interest to us. The chosen deviance function is based upon D_i, the proportional change in A:

$$D_i = (A_i^+ - A_i^-)/A_i^0$$

N.B. the superscripts denote the increase, decrease or default value of the parameter i which are used to generate the phenology. For simplicity, we undertook the analysis using weather data for a single location (Koorlong). Because we have chosen to examine the sensitivity with respect to the emergence date of the first adults, parameters associated with adults have been omitted from the analysis. The results given in Table 4 indicate that the sensitivity values for most parameters are very low, with a maximum value of 8% change in the date of first adult emergence as a result of the 10% change in the Optimal Temperature for Development of fifth instar larvae to pre-pupae stages. These results indicate that GumMoth does not contain any highly sensitive parameters that can unduly affect the phenological predictions of the model.

A plantation of bluegums represents a spatially and temporally limited resource for M. privata. While individual plantations may cover many hectares, they can be established in regions isolated from native forests (e.g. on ex-pasture sites) or other plantations where populations of M. privata may occur. Consequently, a new plantation may not be colonised by fecund females in the first moth-active season after establishment. Delays in colonising new plantations reduce the potential for future local population increase by M. privata because bluegum plantations also represent a temporally limited resource. Bluegums only produce abundant juvenile foliage for four to five tree-growth seasons after establishment. Adult M. privata are unlikely to be attracted to bluegum plantations bearing adult foliage because

females prefer not to oviposit on such leaves (Steinbauer, 2002). Given this scenario, populations of M. privata have a maximum of four to five moth-active seasons in which sufficient individuals have to mature in order to lay enough eggs on each tree in a plantation such that they experience severe defoliation (> than 50% per tree, i.e. the symptom of an outbreak). Haukioja et al. (1988) noted that populations of Epirrita autumnata had large growth rate potentials because females could lay up to 250 eggs, e.g. a 125-fold potential for increase per generation at this fecundity. Similarly, given that individual M. privata can lay well in excess of 300 eggs (Steinbauer et al., 2001), a small number of spring/summer adults may hasten population increase. Our simulations have shown that one or more generations of adults can arise when populations begin to develop early in the moth-active season (i.e. before autumn), primarily because development will be continuous until the autumn equinox (Table 2). Consequently, if increased voltinism coincides with early plantation colonisation and poor regulation by natural enemies, we suggest that the likelihood of an outbreak will be heightened. In considering the role of insect diapause on the development of outbreaks, Nylin (2001) wrote: "In life history terms, when diapause is averted in a large fraction of individuals, the average age at first reproduction is drastically lower, generation times are shorter and there is a larger capacity for population increase." This is the crux of the concept we have attempted to annunciate and provide evidence in support of in this work. Although this may appear obvious to some, we are the first in Australia to postulate this as a factor that could contribute to outbreaks.

Even though M. privata is endemic to predominantly temperate regions of Australia, considerable variation in environmental suitability (mostly of their host trees) occurs each year. We suggest that this variability has provided the selection pressure for the phenological plasticity we have documented in M. privata (Roff, 1983). Specifically, M. privata females prefer to lay eggs on current year's foliage (Lukacs, 1999). Generally, fewer eggs are laid on

tougher leaves than on softer leaves (Steinbauer, 2002). These preferences are reflected in the poor performance of larvae when forced to feed on leaves that are tougher than the current year's foliage (Steinbauer, 2002). Leaf production by Eucalyptus globulus responds to the availability of soil moisture (Metcalfe et al., 1990; Osorio et al., 1998). Consequently, suitable hosts will produce different quantities of leaves in any one tree-growth season and, as a result, be of varying attractiveness to females as well as having different larval carrying capacities. If M. privata had a tightly regulated phenology throughout its range then it is likely there would be more localities and moth-active seasons when populations could not be supported. However, by exhibiting phenotypic plasticity that may correlate with leaf production patterns of the hosts, M. privata may improve its chances of sustaining populations in different localities in all moth-active seasons. We suggest that additional study is needed into the termination of pupal aestivation by temperature and/or soil moisture to improve our predictive capabilities concerning the timing of M. privata activity.

GumMoth clearly illustrates the need to monitor (e.g. using light or other trapping techniques) populations of M. privata in plantations, in particular during the first four to five tree-growth seasons after planting. In addition, we have shown that foresters should monitor for the moth throughout late spring, summer and autumn. Presently, little monitoring is conducted and it is always confined to autumn. If this continues foresters should expect damaging populations of larvae to "sneak-up" on them on occasions because the onset of population growth in late spring and early summer is not being detected. By monitoring for M. privata and getting dates for the start of population growth, foresters could use GumMoth to determine the number of generations the insect is likely to achieve in that moth-active season and year. In this way it would be possible to track the numbers of generations achieved by M. privata in newly established plantations and thereby estimate the risk of large populations arising in the third to fifth years after planting. That is, if the degree of voltinism

in a young plantation continues to exceed 1.0 generation per year for two or more years, such plantations should be considered at greater risk of an outbreak and therefore be surveyed more thoroughly than others where the rate of population increase has been less. Lastly, GumMoth will help reduce the mystery in the minds of foresters concerning the timing of activity (i.e. the phenological plasticity) of M. privata because it will allow them to see for themselves the interplay between the insect's development and ambient temperature and photoperiod.

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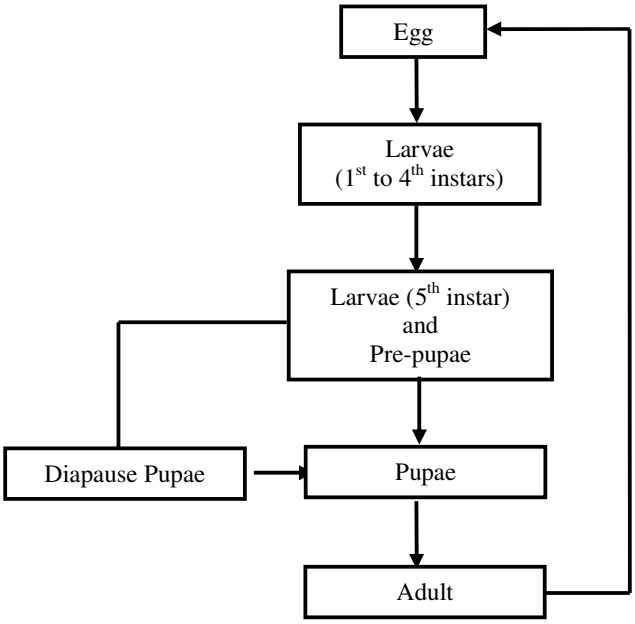
Fig. 1. Schematic diagram of the life cycle of Mnesampela privata as condensed for use in the phenological model. Pre-pupae that experienced one or more weeks development at < 12 hrs daylength undergo pupal diapause prior to adult differentiation (as pupae), otherwise they proceed directly to pupae.

Fig. 2. Schematic diagram of how the duration of pupal diapause in Mnesampela privata may vary during a year. The importance of the autumnal equinox is considered in the Discussion.

Fig. 3. Numbers of generations and phenological patterns predicted for Mnesampela privata using DYMEX based on: (A) first catch (26 February 1999) of adult moths and (B) last catch (28 May 1999) of adult moths at Koorlong. Notice in (A) diapause occurs in both generations and there are two generations of adults and in (B) diapause occurs in the first generation and there is only one generation of adults. Key to compartments (top to bottom, respectively): temperature cycle; log numbers of specified life cycle stages (larval instars identified as L1 to L5, pre-pupae as PP and pupae as P) including photoperiod (third panel, on Y-axis on RHS) during diapause-sensitive first to fourth larval instars.

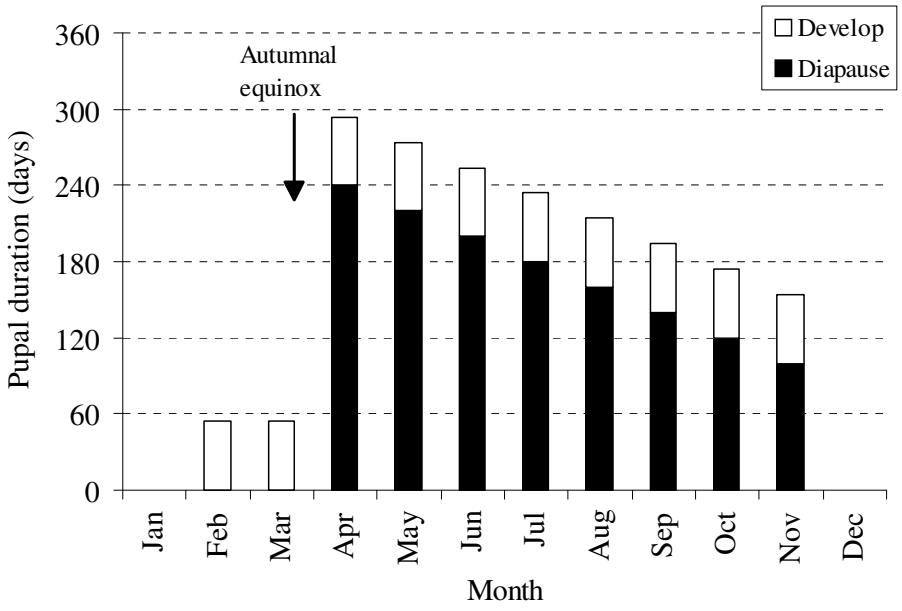
Fig. 4. Southern Australia showing: (A) the region of endemism of Mnesampela privata, and (B) locations where spring/summer (as well as autumn) activity has been recorded (see also Table 3).

1 Fig. 1.


Egg
Larvae
(1st to 4th instars)
Larvae (5th instar)
and
Pre-pupae
Diapause Pupae
Pupae
Adult

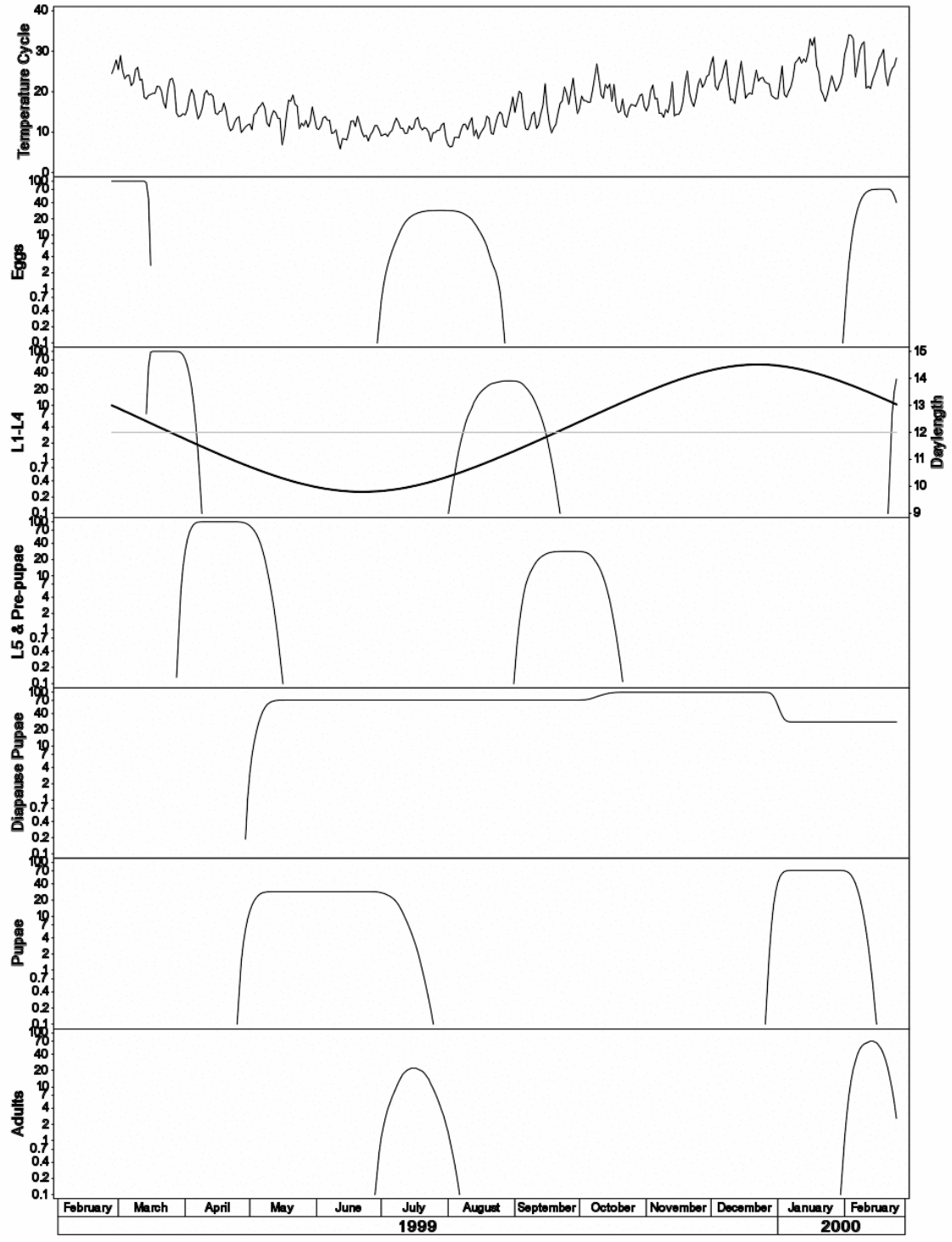
2

1 Fig. 2.

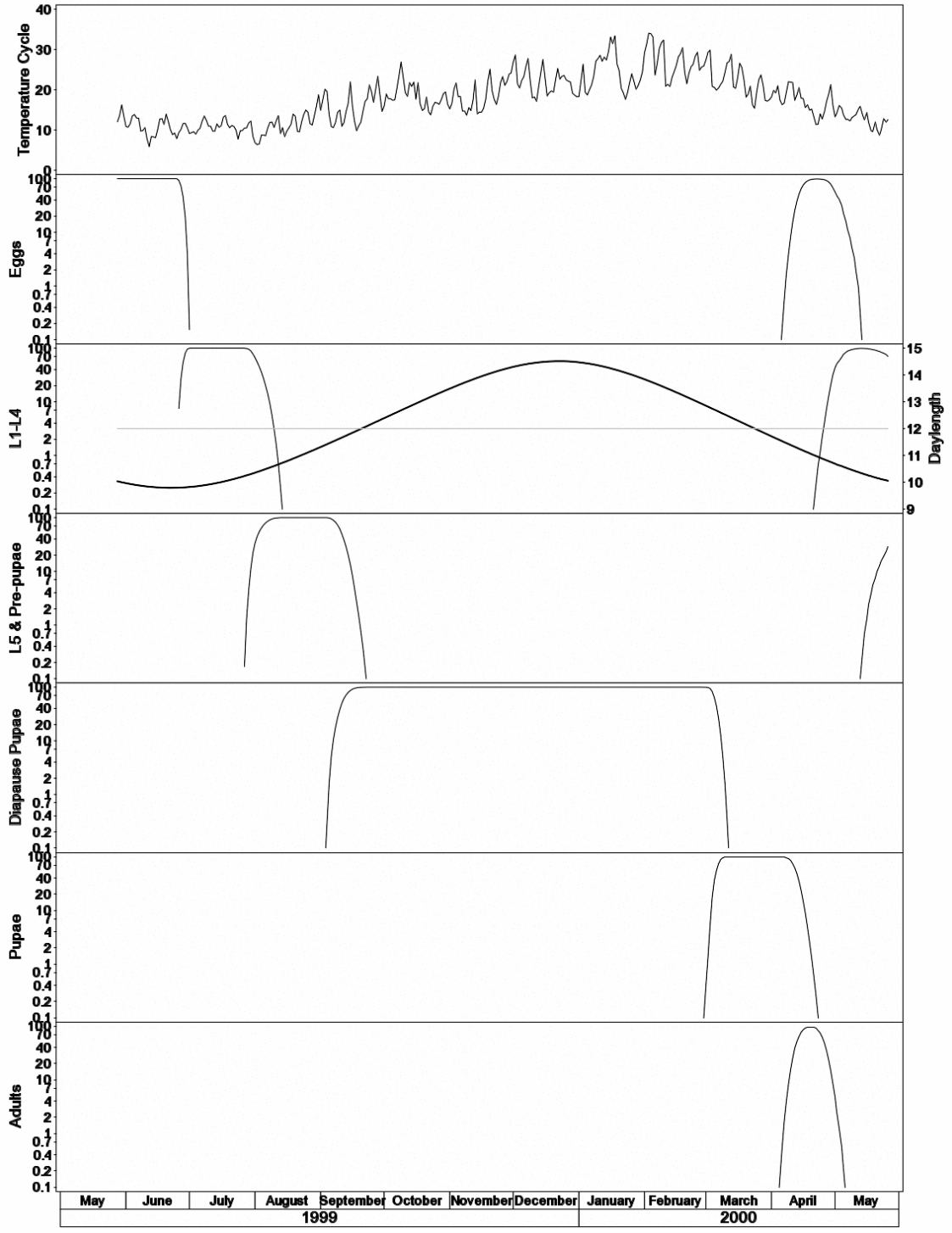

Develop
Diapause
Autumnal equinox
Pupal duration (days)
360
300
240
180
120
60
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

2

Fig. 3A.

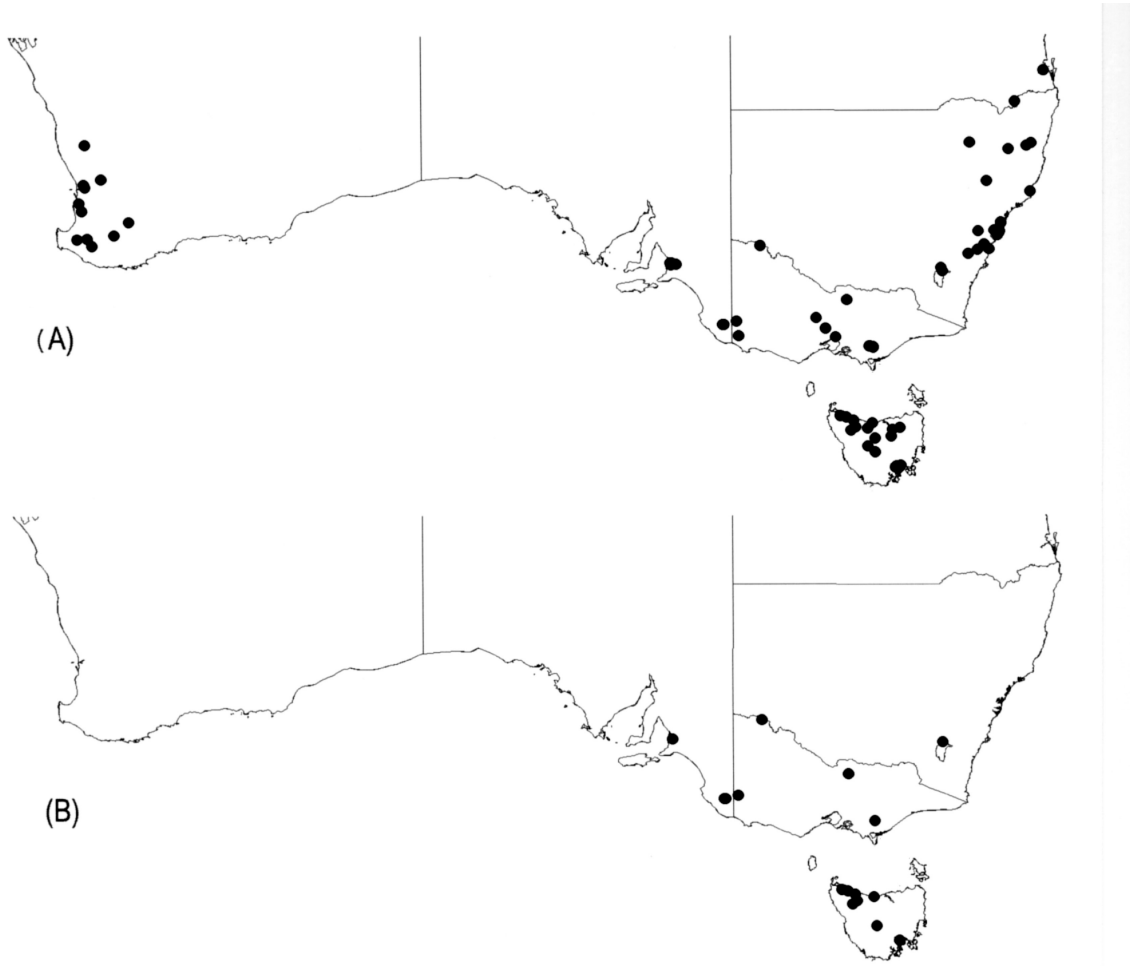

Temperature Cycle
Eggs
L1-L4
Daylength
L5 & Pre-pupae
Diapause Pupae
Pupae
Adults
February
March
April
May
June
July
August
September
October
November
December
January
February
1999
2000

1 Fig. 3B.
2


Temperature Cycle
Eggs
L1-L4
Daylength
L5 & Pre-pupae
Diapause Pupae
Pupae
Adults
May
June
July
August
September
October
November
December
January
February
March
April
May
1999
2000

3

1 Fig. 4.
2



3

Table 1

Developmental temperature thresholds (T_o) and degree-day requirements (K) for immature Mnesampela privata

Life cycle stages	Regression equation for daily development rate (day^{-1}) used to estimate T_o	Estimated T_o (°C)	Average K above T_o for complete development
Eggs	0.006·T - 0.0342 $r^2 = 0.9808$	5.7	165.26 ± 6.86
L1 to L4 instar larvae combined	0043·T - 0.0208 $r^2 = 0.8773$	4.8	240.96 ± 30.32
L5 instar larvae to pre-pupae combined	0.0071·T - 0.0216 $r^2 = 0.656$	3.0	414.41 ± 51.12
Pupae (post & non-diapause)	0.2333·T – 1.4344 $r^2 = 0.759$	6.1	428.65 ± 40.29

Values of K are means ± SD.

Table 2

Paired comparisons of the numbers of generations of adults and phenologies of pupae of Mnesampela privata based on known catch dates for adults that occurred during the same moth-active seasons (or 365-day period)

Simulation pair (along row)	Location place name & state	Elevation (m a.s.l.)	First catch dates ('a')	Number of generations possible after first catch	Generation(s) undergoing diapause	Last catch dates ('b')	Number of generations possible after last catch	Generation(s) undergoing diapause	Sources for dates
1	Wallaroo Rd, A.C.T.	615	26 Nov 1999 spring	2 (Feb-Mar & Oct-Nov 2000)	2nd only	**4 Apr 2000 autumn**	1 – following moth-active season (Mar onwards 2001)	all diapause	1
2			28 Nov 2000 spring	1 – within same moth-active season (Mar-Apr 2001)	no diapause	**20 Mar 2001 autumn**	1 – following moth-active season (Feb onwards 2002)	all diapause	
3	Ringwood, Tas.	540	16 Dec 1980 summer	2 (Apr-Jul & Oct-Dec 1981)	no diapause	3 Feb 1981 summer	1 – following moth-active season (Dec 1981-Jan 1982)	no diapause	2
4	Stoney Rise, Tas.	70	5 Nov 1994 spring	2 (Feb-Mar, Oct onwards 1995)	2nd only	13 Aug 1995 winter	2 (Jan-Feb & May onwards 1996)	no diapause	3
5			5 Nov 1996 spring	1 – within same moth-active season (Feb-Mar 1997)	no diapause	4 Jun 1997 winter	no adults*	all diapause	
6	Surrey Hills, Tas.	612	28 Nov 1995 spring	no adults#	no diapause	14 Feb 1996 summer	no adults†	all diapause	4
7	Koorlong, Vic.	52	26 Feb 1999 summer	2 (Jun-Aug 1999 & Jan onwards 2000)	all diapause	**28 May 1999 autumn**	1 – following moth-active season (Apr-May 2000)	all diapause	5
Number of generations				11			8		
Number of generations diapausing					4 (36%)			5 (63%)	

DYMEX predictions were run for 365d from each catch date; months of simulated adult activity in parentheses. DYMEX simulations based on the catch dates for Koorlong are illustrated in Fig 3.

Key to sources for first and last catch dates: 1, Steinbauer, 2003; 2, de Little, in lit.; 3, Hill, in lit.; 4, Lukacs, 1999; 5, Ebner and Rhind, in lit.

*adults emerge in June 1998 after 1 year and 1 month (or approximately 390d); #adults emerge in December 1996 after 1 year and 1 month; †adults emerge in March 1997 after 1 year and 2 months (or approximately 490d)

Table 3

Summary of locations where spring/summer (as well as autumn) activity by Mnesampela privata has been recorded

Location place name	State	Sources	Grid reference	Altitude (m a.s.l.)	Year(s)	Incidence of outbreaks/populations warranting insecticide control
Wallaroo Rd	A.C.T.	1	35°09'S 145°02'E	615	1998/99 to 2001/02 inc.†	locally abundant (1999 to 2002 moth-active seasons inc.; complete defoliation of isolated E. globulus and E. rubida)
Blackwood	S.A.	6	35°01'S 138°37'E	260	-	n/a
Geraghty	S.A.	7	37°20'S 140°39'E	30-50	2001/02	population warranting insecticide control (2002; E. globulus)
Greenview	S.A.	7	37°20'S 140°40'E	30-50	2001/02	population warranting insecticide control (2002; E. globulus)
Reilly	S.A.	7	37°20'S 140°37'E	30-50	2001/02	population warranting insecticide control (2002; E. globulus)
Strother	S.A.	7	37°20'S 140°38'E	30-50	2001/02	population warranting insecticide control (2002; E. globulus)
Calder	Tas.	8	41°05'S 145°38'E	150	2001/02	n/a
Hobart	Tas.	9	42°53'S 147°20'E	50	-	n/a
Irishtown	Tas.	8	40°54'S 145°08'E	200	2001/02	n/a
Mawbanna	Tas.	8	40°57'S 145°21'E	210	1999/00 & 2000/01	n/a
Ringwood	Tas.	2	41°19'S 145°43'E	540	1979/80	population warranting insecticide control (February 1981; 5-year old E. nitens)
Stoney Rise	Tas.	3	41°11'S 146°21'E	70	1993/94 & 1995/96	n/a
Surrey Hills	Tas.	2, 4	41°27'S 145°32'E	612	1994/95 & 1995/96	serious outbreak (December 1993 & April 1994; 56 ha of 2-year old E. nitens severely defoliated)
Tarraleah	Tas.	4	42°18'S 146°27'E	589	1994/95 & 1995/96	n/a
Allambi	Vic.	7	37°12'S 141°09'E	100-150	2001/02	population warranting insecticide control (2002; E. globulus)
Koorlong	Vic.	5	34°17'S 142°05'E	52	1998/99 & 2002/03	serious outbreaks (April to June 1998, March to May 1999 & February to April 2003; complete defoliation of non-insecticide treated E. grandis)
Shepparton	Vic.	4	36°23'S 145°24'E	110	1995/96 & 1996/97	n/a
Yallourn	Vic.	4	38°12'S 146°24'E	155	1995/96 & 1996/97	n/a

All records except those from Wallaroo Rd, Blackwood, Hobart and Stoney Rise are from commercial plantations; Fig. 4B illustrates locations of place names cited herein.

Key to sources: 1, Steinbauer, 2003, Steinbauer pers. obs.; 2, de Little, in lit.; 3, Hill, in lit.; 4, Lukacs, 1999; 5, Ebner et al., in lit.; 6, McFarland, 1988; 7, Anning and Bulinski, pers. comm.; 8, Rapley, pers. comm.; 9, Elliott and Bashford, 1978

†Spring/summer activity not observed during 2002/03.

Table 4

Results of the GumMoth sensitivity analysis. The deviance value $\underline{D_i}$ indicates the proportional change in the number of days from egg to adult emergence as a result of a 10% change in the corresponding parameter value. The default duration from egg to first emergence was 96 days at Koorlong for eggs laid on 5 November 1996

Life cycle cohort	Model Parameter	$\underline{D_i}$
Egg	Base Temperature for Development	0.01
	Optimal Temperature for Development	0.03
	Supra-optimal Development Slope	0
	Threshold Development Heat Sum (degree days)	0.02
First to Fourth Instar Larvae	Base Temperature for Development	0.01
	Optimal Temperature for Development	0.05
	Supra-optimal Development Slope	0.01
	Threshold Daylength for Diapause Induction	0
	Threshold Daylength	0
	Threshold Development Heat Sum (degree days)	0.03
	Development Rate (degree days^{-1})	0
Fifth Instar Larvae to Pre-pupae	Base Temperature for Development	0.01
	Optimal Temperature for Development	0.08
	Supra-optimal Development Slope	0.01
	Threshold Development Heat Sum (degree days)	0
	Diapause Induction Transfer Rate (degree days^{-1})	0
	Diapause Induction Threshold Days < X hours daylength	0
	Non-diapause Pupation Threshold Development Heat Sum	0.03
	Non-diapause Pupation Threshold Days < X hours daylength	0
Diapause Pupae	Maximum Degree Days	0
	Rate of Decline in Diapause Duration (day^{-1})	0
	Transfer Rate (day^{-1})	0
Non-diapause Pupae	Development Base Temperature	0.02
	Optimum Development Temperature (C)	0.05
	Supra-optimal Development Heat Accumulation Rate	0.01
	Minimum Degree Days for Full Development	0.03
	Transfer Rate (degree days^{-1})	0